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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Abstract

Populations of fish eating mammals (primarily seals) and birds have increased in the Baltic Sea and there is concern that their consumption reduces fish stocks and has negative impact on the fishery. Based primarily on published data on fisheries' landings and abundances, consumption and diets of birds and seals around year 2010, we compare consumption of commercial fish species by seals ($1*10^5$ metric tons per year) and birds ($1*10^5$ tons) to the catch in the commercial and recreational fishery ($7*10^5$ tons), and when applicable at the geographical resolution of ICES subdivisions. The large populations of herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and cod (*Gadus morhua*), primarily inhabit off-shore areas and are mainly caught by the fishery. Predation by birds and mammals likely has little impact on these stocks. For these species, seals and birds may be negatively impacted by competition from the fishery. In the central and southern Baltic, seals and birds consume about as much flatfish as is caught by the fishery and competition is possible. Birds and seals consume 2-3 times as much coastal fish as is caught in the fishery. Many of the coastal species are not much targeted by the fishery (e.g. eelpout *Zoarces viviparus*, roach *Rutilus rutilus* and ruffe *Gymnocephalus cernua*), while other species used by wildlife are important to the fishery (e.g. perch *Perca fluviatilis* and whitefish *Coregonus* spp.) and competition between wildlife and the fishery is likely, at least locally. Estimated wildlife consumption of pike (*Esox lucius*), sea trout (*Salmo trutta*) and pikeperch (*Sander lucioperca*) varies among ICES subdivisions and the degree of competition for these species will likely differ among areas. Our results indicate that competition between wildlife and fisheries need to be addressed in basic ecosystem research, management and conservation. This requires improved quantitative data on wildlife diets, abundances and fish production.

Keywords

Baltic Sea, bird, catch, competition, fisheries, food consumption, seal

Introduction

The exploitation of many fish stocks is intensive, and for many years overfishing has been on the political agenda (e.g. UN, 2002; EU, 2009). With recreational fishing as a fast growing component of the tourism-industry, increasing fishing pressure must be expected also on other species than those targeted by commercial fisheries (Coleman *et al.*, 2004; Lewin *et al.*, 2006; Ihde *et al.*, 2011).

There is increasing awareness that fish are vital to the functioning of aquatic ecosystems (Crowder *et al.*, 2008; Cury *et al.*, 2011; Jensen *et al.*, 2012; Morissette *et al.*, 2012; Östman *et al.*, 2016) and fish sometimes even impact terrestrial environments (Hilderbrand *et al.*, 1999; Moore and Schindler, 2004). Consequently, it has become generally accepted that fisheries need to be managed using an ecosystem approach (EU, 2009; Essington and Punt, 2011). Acknowledging that “stakeholders” other than humans play an important role, focus turns to the potential competition between humans and other fish consumers, such as marine mammals and birds. Numerous studies have addressed the possibility of increasing fishery by reducing abundances of competitors, as well as the impact of fisheries on the foraging conditions of top predators (e.g. Corkeron, 2004; Pikitch *et al.*, 2004; Cury *et al.*, 2011; Morissette *et al.*, 2012; Bowen and Lidgard, 2013; Hilborn *et al*., 2017).

In the Baltic Sea, issues of competition between fishery and predatory (fish eating) wildlife have been considered for at least two centuries. When inexpensive Norwegian whale oil flooded the market in the end of the 19th century the production of seal oil became unprofitable, reducing hunting (Harding and Härkönen, 1999). As a consequence, seals became considered competitors rather than resources and bounty systems were initiated to reduce the seal populations (Sweden 1903-1967, Denmark 1889-1977, Finland 1909-1975).

Hunting reduced the ringed seal (*Pusa hispida*) population from about 180 000 in the beginning of the 20th century to about 25 000 in the 1940s. Grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) decreased from about 80 000 to 20 000 (Harding and Härkönen, 1999) and 5 000 to 500 (Härkönen and Isakson, 2010) individuals, respectively. After the closure of the bounty systems, organochlorine pollutants (mainly PCB and DDT) brought the populations close to extinction through diseases and sterility (Bergman and Olsson, 1985; Bergman, 1999). All Baltic seal species plunged and only some 3 000 grey, 2 000-3 000 ringed and 200 harbour seals remained in the 1970-80s (Harding and Härkönen, 1999; Härkönen and Isakson, 2010). Drastic reductions in the levels of these toxic substances have since improved the health of the seals (Bergman, 1999; Bäcklin *et al.*, 2011) and since the late 1980s populations have increased by 6-9% annually (Harding *et al.*, 2007).

Seals are not the only fish predators that have increased over the last decades. From being nearly absent from the Baltic in the beginning of the 20th century, the population of the great cormorant (*Phalacrocorax carbo sinensis*) has increased from some 6 500 nesting pairs in 1981 to >150 000 pairs in 2006-2012 (Herrmann *et al.*, 2014). This rapid increase is parallel to that recorded across Europe (Carss, 2003; Bregnballe *et al.*, 2014).

With growing populations of seals and cormorants, their impacts on fish stocks and possible exploitative competition with commercial and recreational fisheries have become increasingly discussed. Public debates are sometimes heated. Some fisheries stakeholders demand culling to reduce cormorant and seal populations, while some conservationists advocate for sustained protection.

One reason for the strong polarization in the debate is the lack of data on fish consumption by predators and the fishery catch, as well as of estimates of their effects on fish populations. The objective of this paper is to collate and present quantitative data on fish extraction by the fishery, mammals and birds – how much are caught in different parts of the Baltic Sea, and of which fish species. These quantitative data constitute the results section of this paper, and in the discussion we combine our data with estimates of fish production and published studies on the impacts of fishery, seals and birds on fish Baltic Sea fish stocks. This synthesis will hopefully support a more informed debate on resource competition between wildlife and humans and provide relevant information for resource management.

Material and Methods

The data used in the analyses have been derived from a multitude of sources: scientific publications, reports and unpublished information. Abundances of birds and aquatic mammals, and the fishery catch are from around year 2010, depending upon data availability. The full derivation of all data is described in three supplementary documents, each focusing on one of the three consumer groups (S1=mammals, S2=birds, S3=fishery). Due to data scarcity and uncertainties, consumption and catch estimates are coarse, but the data used are the best available given the geographical resolution and extent of the study, covering spatial scales from regional to whole basins.

Discards have not been included in the catch as data are uncertain or missing, in particular for coastal species. No assumptions have been made on the quantities of fish mortally wounded but not consumed by birds and seals (c.f. Davis *et al*. 1995; Adámek *et al*. 2007; Kortan *et al*. 2008; Bergström et al. 2016).

Estimates of fish consumption by mammals and birds were done in two steps. First, abundances of predatory birds and mammals were compiled for areas corresponding to subdivisions (SD24-32, Figure 1). Second, these abundance data were combined with consumption rates and diet compositions to derive estimates of the extraction of different fish species. Depending on the population structure of different fish species and the spatial resolution in the data on fishery catch, the geographic scale at which these extraction rates are presented vary from the entire Baltic to individual ICES subdivision.

Six predatory mammals were considered: grey seal, ringed seal, harbour seal, American mink (*Neovison vison*), harbor porpoise (*Phocoena phocoena*) and common otter (*Lutra lutra*). For birds, fish consumption was estimated for 21 species. Data on abundances, diets and estimated consumption rates for mammals and birds are in supplementary documents S1 and S2.

Fishery landings were estimated separately for the commercial and recreational fishery (S3). Data on the commercial catch were mainly based on information from ICES. Landings by anglers are not as well documented, but for Estonia, Finland, Russia and Sweden, covering most of the Baltic coast there are assessments available.

Exploitative competition between fisheries and wildlife occurs if the catch/consumption of a fish species by one group has adverse effects on another consumer group. Field observations of decreased abundance of a fish species in response to fisheries and/or predation by wildlife imply exploitative competition. Reduced catch caused by wildlife's interference with fishing gear is not considered in this paper.

Estimates of effects of predation and fishery on fish populations should ideally be based on consumption vs. production rates. Production rates are difficult to derive for fish as abundance measurement and age structure data often are of poor quality or missing, in particular for coastal species consisting of local populations. In addition, compensatory processes such as increased growth and/or survival of juveniles in response to increased fisheries/predation (Rose *et al.*, 2001) complicate analyses. Production in populations that are lightly exploited may increase as a result of increased fishery but at some point compensatory processes cannot compensate for further mortality increases. At this point production decreases and the decrease in population size accelerates (e.g. Hilborn and Walters, 1992).

If possible, and as described above, catch and consumption should be compared to production estimates. For sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) which together have been suggested to constitute some 80% of the Baltic Sea fish biomass (Elmgren, 1984; Thurow, 1984), there are production estimates based on ecosystem analyses. Elmgren (1984) proposed a fish production of 11-12 metric tons per $km^2 * yr^{-1}$ for the Baltic Proper (SD24-29) and the Gulf of Finland (SD32), and 7.6 and 2.8 tons for the Bothnian Sea (SD30) andthe Bothnian Bay (SD31). Of the production, landings in fisheries corresponded to 24-26%, 15% and 10% in the three regions respectively. Based partly on data from Elmgren (1984) but with more data on fish and fisheries, Harvey *et al.* (2003) reported production estimates of 3.7, 2.9 and 1.3 tons per km^2 for sprat, herring and cod in the Baltic Proper and Gulf of Finland (SD25-29+32). . Fisheries on these populations extracted on average 16%, 29% and 47%, respectively, of the production. Tomczak *et al.* (2012) modified the model of Harvey *et al.* (2003) and calibrated it to a longer period (1974-2006). They estimated the total annual production by sprat, herring and cod to 16 tons per km^2 with the fishery extracting 20%, 15% and 43% of the production of these species. Wolnomiejski and Witek (2013) presented a detailed ecosystem analysis on the Szczein Lagoon and derived at a fish production of ~45 tons per km^2 based on a primary production and a net allochthonous supply of 730 gC/m^2. Using the relationships between primary- and fish production reported in these ecosystem analyses, and a primary production of 165gC/m^2 in the Baltic Proper (Elmgren, 1984; consistent with intensive pelagic monitoring up to and including recent years, pers. comm. with U. Larsson, Dept. Ecology, Environment and Plant Science, Stockholm, Sweden), the fish production would be ~10 tons per km^2.

During the periods studied by Harvey *et al.* (2003) and Tomczak *et al.* (2012) the abundance of seals was lower than today and their predation impact was found rather insignificant, while fisheries for at least herring and cod had adverse impacts on these populations (ICES, 2015). The calculations thus indicate that extractions by fishery and predators exceeding 20-40% of the production can significantly reduce a Baltic Sea fish stock. For lakes, it has been suggested that fishing is generally sustainable at catch rates corresponding to <15% of the biomass (Downing and Plante, 1993), and as production is usually around 50% of the biomass (Downing and Plante, 1993; Randall and Minns, 2000), this corresponds to an extraction level of 30%. An extraction of 20-40% of the production will be used as reference point when discussing impacts on fish populations and competition between fishery, mammals and birds.

Results

Annual fishery landings add up to 7*10^5 tons (Table 1) and the combined predation by mammals and birds amounts to 2*10^5 tons (1*10^5 tons for each group). Humans thus extract four times more fish than seals and birds combined. Among the marine mammals, the three seal species account for >95% of the consumption (Table S1.1). Five species of birds, cormorant, razorbill (*Alca torda*), common guillemot (*Uria aalge*), common and red-breasted merganser (*Mergus merganser* and *M. serrator*) account for 80% of the consumption by birds (Table S2.1). Focus in this paper will be on humans, seals and these five bird species.

The fishery catch is dominated by sprat, herring and cod, which together contribute ~95% of the total landing. These three fish species constitute ~60% of the consumption by seals and ~30% of the consumption by birds (Table 1). With the exception for the Bothnian Bay, where the fishery for sprat, herring and cod is limited, consumption by birds and seals is small in comparison to the catch.

Predation by seals is dominated by the grey seal (~75% of the total consumption), followed by ringed seal (~20%) and harbour seal (~5%). The estimated food consumption of grey seal consists generally of about 50% herring and 10% sprat, while eelpout (*Zoarces viviparus*), cod and cyprinids each constitute ~5% (Table S1.6). In the diet of ringed seal, herring, vendace (*Coregonus albula*) and three-spined stickleback (*Gasterosteus aculeatus*) constitutes about 40%, 30% and 20% respectively. Harbour seals feed primarily on herring (40%), but also substantially on flatfish (20%) and sprat (10%).

Among the five bird species, consumption by the cormorant constitutes 50% of the combined consumption, while razorbill and common guillemot together consume 30% and the mergansers 20%. The cormorant's diet is diverse, consisting of mainly coastal species, with on average 25% perch (*Perca fluviatilis*) and 10-15% each of eelpout, roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernua*, Table S2.6). Diets of razorbill and common guillemot is dominated by sprat (90%), with herring and other fish species each constituting 5%. Data on merganser diets are poor, but they are still included in the analyses (100% unspecified fish) since they contribute substantially to birds' fish consumption.

Overall, on a Baltic Sea scale, the fishery catch is considerably larger than the predation by birds and seals combined (see above). The situation is different in coastal areas, however, where birds annually consume about $4*10^4$ tons and seals $1*10^4$ tons of coastal species (all species except for cod, herring, sprat, flatfish and salmon (*Salmo salar*)). The combined consumption by seals and birds is thus substantially higher than the catch of coastal species ($2*10^4$ tons). To derive these numbers, razorbill and common guillemot were assumed to feed exclusively on off-shore species. Mergansers, for which diet data are lacking, were assumed to include 50% coastal fish species in their diet, which is a conservative estimate given that they are primarily residing and foraging in shallow coastal areas. Unspecified fish in cormorant and seal diets was split into offshore and coastal fish in proportion to the quantity of identified prey from these two categories in their diets. To avoid underestimating the fishery impact, all unspecified landings were assumed to be coastal species.

In a comparison for the entire Baltic Sea, the combined consumption by predators is in the same range as the fishery catch for seven of twelve fish species (salmon, sea trout, eel (*Anguilla anguilla*), perch, northern pike, pikeperch and whitefish, Figure 2). To evaluate if this implies resource competition, other factors and data need to be considered and this is done in the Discussion section.

Discussion

Our results show that both seals and birds consume large quantities of fish and should to be carefully considered in ecosystem analyses and stock assessment models. This is particularly true for local, coastal fish populations. These populations are often small, at the same time as they are overlapping spatially with the haul-out sites for seals and feeding areas for many avian predators (three of the five consumers considered here; cormorant and the mergansers). The impacts of wildlife on the larger, off-shore populations are small compared to the fishery. However, as these fish stocks are intensively exploited by the fishery, the additional mortality caused by growing seal populations also deserve to be accounted for in resource management.

In the following, we will first focus on the extraction of fish species with a single or few populations (cod, herring, sprat, eel, flatfish and salmon) and then shift to coastal species which are reasonably sedentary, consisting of local populations. If results differ substantially among ICES subdivisions, this indicate that care is necessary when interpreting our results. For example, the estimated consumption of sea trout by seals is equal or exceeds the catch in four subdivisions, while they appear to consume no sea trout at all in four other subdivisions (Table 1). The explanation is that total consumption by seals is large and even a small proportion (1%) of sea trout in the diet results in an estimated consumption that is substantial compared to the catch. Predation impact on species that are rare it the diet are thus associated with substantial uncertainties.

The largest fish stocks (cod, herring and sprat) are under a substantial pressure from commercial fishery (ICES, 2015) while predation by seals and birds are generally small in comparison (Table 1). The fishery for these species is not in substantial competition from birds and/or seals, whereas birds and seals may be subjected to competition from the fishery. However, since these fish populations are impacted by fisheries, increased mortalities caused by seals and birds, without reductions in the fishery, may contribute to a total mortality rate that exceeds the capacity of compensatory responses.

Recruitment of eel to European waters has decreased by 95-99% over the last thirty years and the species is classified as critically endangered by IUCN (Jacoby and Gollock, 2014). The reason for this decrease is unknown and it is thus not possible to conclude if fisheries, seals and/or birds reduce the population and compete for this species. From a conservation and management perspective it is noteworthy that the predation by cormorants is of the same magnitude as the landings (Table 1).

In the central Baltic Sea (SD27-28), populations of flounder (*Platichthys flesus*) and turbot (*Scophthalmus maximus*) are impacted by the fishery, as shown by changes in abundance and size composition in a no-take area (Florin *et al.*, 2013). In some areas seals and cormorants take at least as much flatfish as the fishery (Table 1) and it is likely that there is competition for flatfish. Theoretical analyses indicate competition between cormorants and fisheries in SD25 and 27 (Östman *et al.*, 2013). More to the south (SD24-26), the catch is substantially higher than the predation by seals and birds.

Salmon and sea trout are intensively fished by both commercial and recreational fishers, and the closure of commercial offshore fishery for salmon has resulted in increased returns of adults to spawning rivers (ICES, 2016). This shows that salmon has been impacted by the fishery. This is likely the case also for sea trout, which has many local populations that reproduce in small streams.

Salmon and trout can also be important prey for seals, as described by Suuronen and Lehtonen (2012) for grey seal in the Bothnian Bay (SD31), and increased grey seal population appears to have reduced the survival of salmon substantially (Mäntyniemi *et al.*, 2012). Furthermore, local sea trout populations consisting of some tens or hundreds of adults are prone to predation effects, as seals have been observed to patrol outside river mouths and also entering into rivers to hunt for ascending fish (c.f. Middlemas *et al.*, 2006). This kind of focused predation is not captured by the broad-scale analyses of the current study. Our data (Table S1.3), in combination with previous studies, suggest that the intensity of the competition varies among different local populations.

A five years closure of the fishery for common whitefish (*Coregonus* sp., excl. *C. albula*) in a coastal area of SD30 resulted in increased catch rates (Florin *et al.*, 2016), indicating that the whitefish stock had been influenced by the fishery. Verliin *et al.* (2013) also suggested that overfishing may explain some of the long-term catch variation in this species. In the Baltic Proper and Bothnian Sea, more whitefish is consumed by grey seals than caught in the fishery (Table 1) and predation by the seals is also substantial in the Bothnian Bay and Gulf of Finland. It is thus likely that fishery and seals compete whitefish in several areas. Vendace (*C. albula*) is primarily fished in the Bothnian Bay (SD31). The fishery is intensive and managed under the assumption that it impacts the population (Andersson *et al.*, 2015). As ringed seal consume more than landed by the fishery (Tables S1.7 and S3.4; Lundström *et al.*, 2014), competition is possible.

Perch is a common species with local populations around the Baltic. There are several studies on effects of cormorant predation on perch and these are summarised in Supplement S4. Even if apparently contradictory, the results from these field studies are rather conclusive. The current fishing intensity can be sufficient to impact perch populations (Bergström *et al.*, 2007) and cormorants and seals together consume twice as much as the fishery (Table 1). Locally, in areas where perch production can be assumed to be very high, no effects of cormorant predation can be detected (Pūtys, 2012). In less productive coastal areas, representative for larger areas of the Baltic Sea, decreases in perch in response to cormorant predation can be detected in long-term data series, provided that the variation in cormorant abundance is large (strong signal) and particularly if data from reference areas allows for background variation to be taken into account (Östman *et al.*, 2012). The local effect of cormorant predation on perch can be substantial (80-90% reduction in perch, Vetemaa *et al.*, 2010; Östman *et al.*, 2012; Gagnon *et al.*, 2015), but there are no data available on how far from nesting sites that effects from cormorant predation can be detected. This distance is likely to depend not only by the size of a colony, but also influenced by the age of the colony (c.f. Gagnon *et al.*, 2015).

Perch and pike (below), are demersal warm water species that inhabit waters above the thermocline (~10 m in coastal areas) during the growth (=production) season. For these species, catch and predation per bottom area shallower than 10 m is thus the relevant spatial unit. Based on our estimates (Table 1) the average extraction of perch exceeds 400 kg/km^2 in areas shallower than 10 m (Table 2). However, as a large proportion of these bottoms are located in the outer coastal zone and off-shore areas where perch is uncommon, the exploitation intensity in archipelagos is generally substantially higher. With an estimated perch production of 2 tons/km^2 (see S4) the local fishing/predation pressure can reach or exceed the level 20-40% of the production (Table 2), which for other Baltic fish stocks have resulted in adverse impacts on the populations (see Material and Methods). These calculations supports the field observations that perch populations are likely to be locally negatively impacted by both fishery and predation from cormorants and in some areas possibly also by seals.

Pike (*Esox lucius*) is sedentary (Saulamo and Neuman, 2002) with genetic differences over relatively short distances (Aro, 1989; Laikre *et al.*, 2005). When quantifying pike in a sheltered bay on the Swedish coast, Adill and Andersson (2006) derived at an biomass estimate of 1000 kg/km^2, resulting in an annual production of 700 kg/km^2 based on an assumed production to biomass ratio of 0.7 (derived from Baltic cod, another fast growing piscivorous species; Harvey *et al.*, 2003). Compared to this production estimate, fishing and predation rates are high (Table 2). This is consistent with increased abundances and larger individuals in response to a local fishing closure (Bergström *et al.*, 2007). In SD25, 27 and 29, the predation by cormorants and seals are in the same order of magnitude as the catch (Table 1) and competition is likely (c.f. Östman *et al.*, 2013). There are also observations of high incidences of seal wounds on pike at spawning sites (Bergström *et al.*, 2016), indicating local effects which are not detected on the spatial scale of this study.

Pikeperch (*Sander lucioperca*) are unevenly distributed along the coast occurs in separate and restricted areas (Lehtonen and Toivonen, 1988; Lehtonen *et al.*, 1996; Saulamo and Thoresson, 2005) and genetic differences have been documented among such areas (Dannewitz *et al.*, 2010; Säisä *et al.*, 2010). Management is generally based on the assumption that populations are significantly impacted by fishery (Mustamäki *et al.*, 2014; Lappalainen *et al.*, 2016). In many areas, the catch have decreased over the last decades, and although under debate (Heikinheimo and Lehtonen, 2016; Heikinheimo *et al.*, 2016; Salmi *et al.*, 2016; Lehikoinen *et al.*, 2017) predation from cormorants has been suggested to contribute to this decline (Mustamäki *et al.*, 2014; Salmi *et al.*, 2015). Pikeperch constitute a small fraction in cormorants' diet and predation estimates are uncertain (Table 1). With the patchy distribution of pikeperch, possible competition among seals, cormorants and fisheries cannot be captured by our large-scale study.

As seen above, competition with wildlife is primarily a potential problem to fisheries for coastal species. For cormorants in general, this is consistent with results from a meta-analysis of a large number of studies on interactions between cormorants and different fish species (Ovegård *et al.*, 2017). However, our results show that landings from the large offshore stocks of herring, cod and sprat, which quantitatively dominate Baltic Sea fishery, were not subject to significant competition from seals and birds. This difference in competition between coastal and off-shore areas, as well as differences among coastal sites, reflects spatial aspect of the issue of competition for the fish. Another spatial aspect is that "Baltic wildlife" can be involved in competition with fishery outside the Baltic Sea. Intensive fishing in the North Sea and other areas may have adverse effects on winter feeding conditions for migratory birds (however, see Hilborn *et al.*, 2017 on fishery effects on small forage fish), influencing their reproductive condition once back in the Baltic. On the other hand, predation by overwintering cormorants has adverse impacts on brown trout, salmon and grayling (*Thymallus thymallus*) in Danish rivers (Jepsen *et al.*, 2014).

Predation by seals and in particular by birds are often excluded from quantitative food web studies, including several of those published on the Baltic Sea (e.g. Elmgren, 1984; Ulanowicz and Wulff, 1991; Sandberg *et al.*, 2000; Worm *et al.*, 2000; Harvey *et al.*, 2003; Håkanson and Gyllenhammar, 2005; Sandberg, 2007; Tomczak *et al.*, 2012). Our results show that both seals and birds can consume large quantities of fish and deserve to be carefully considered in ecosystem analyses and stock assessment models. This is particularly important in areas where populations of fish predators are increasing, particularly in coastal areas where birds and seals concentrate and where many fish populations are local.

Predation by birds can also be an issue for the management of freshwater systems. From Lake Oneida in North American, Rudstam *et al*. (2004) and Coleman *et al*. (2016) reported significant reductions in both yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) abundances in response to predation by the double-crested cormorant (*Phalacrocorax auritus*). Another example is from Danish rivers, in which cormorant predation reduced salmon smolt output by 50 % in just few weeks (Jepsen *et al.* 2010, 2014). Such short time "predation events" can easily be overlooked in ecosystem models with focus on the large scale picture, but can be very significant to consider in management. As emphasised by Essington and Plaganyi (2013), it is important that models include the interactions that are critical to the questions that they are supposed to address. Straight forward and reasonably detailed calculations like ours, can produce insights that are difficult to derive from complex models where detailed aspects of trophic interactions may have to be sacrificed when constructing the models (c.f. Hilborn *et al.* 2017).

In the Ecopath with Ecosim (EwE) food–web model Harvey *et al.* (2003) assumed that herring sprat and cod together constituted 50% of the seal diet in SD25-29. This assumption was also used in the updated EwE model of Tomczak *et al.* (2012), who calculated seals to consume $1*10^4$ tons of herring sprat and cod in 2006. Our compilation of data suggests that these three fish species constitute ~70% of the seals diet and that they consumed $5*10^4$ tons in 2010 (Table 1). The five fold difference in consumption results from our use of a higher proportion of herring sprat and cod in the seal diet and a larger population of seal.

In conclusion, our results show that there are cases of competition between wildlife and fisheries in the Baltic Sea, although not for all species and not to the same extent everywhere. There are many uncertainties, e.g. how far from cormorant colonies perch abundances are adversely impacted and how much of marginal diet components (e.g. salmon, sea trout, eel, pikeperch) are actually consumed. There are also uncertainties regarding the potential for compensatory mechanisms in the fish populations, in particular if wildlife feed on smaller sizes than exploited by the fishery. Besides comprehensive and comparative analysis over large systems, such as our analyses, one way to improve our understanding of the importance of competition is to explore the responses in the fish community to changes in the management (c.f. Lessard *et al.*, 2005) or to changes in local predator populations.

Supplementary material

The following supplementary material is available at ICESJMS online:

S1 – Supplement 1, Fish consumption by aquatic mammals

S2 – Supplement 2, Fish consumption by birds

S3 – Supplement 3, Fishery catch

S4 – Supplement 4, Review of published studies on cormorant predation on perch

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Table 1. Distribution among ICES subdivisions 24-32 (Figure 1) of fishery catch (metric tons, based on Table S3.4) and consumption by seals (Table S1.7) and birds (Table S2.7, only cormorant, razorbill, common guillemot, common and red-breasted merganser). For some fish, primarily open sea species we assume a common population for the entire Baltic Sea and catch/consumption are summed over subdivisions, while catch/consumption for other species are divided into subdivisions. The fish species that are presented separately are of interest to commercial and recreational fisheries. The category "unspecified" may include species that are also reported separately. Total estimated consumption by e.g. mergansers is almost 19 000 tons and without diet composition data this quantity cannot be attributed to different prey species.

fish species	consumer group	ICES subdivision SD24	SD25	SD26	SD27	SD28	SD29	SD30	SD31	SD32	entire Baltic
cod	fishery	8 900	50 000								59 000
	birds	1 100	530								1 600
	seals	1 600	3 400								4 900
herring	fishery	15 000	150 000					72 000	2 100	incl. in SD25-29	240 000
	birds	500	2 300					800	63		3 600
	seals	300	36 000					4 200	7 600		48 000
sprat	fishery	350 000									350 000
	birds	22 000									22 000
	seals	8 300									8 300
flatfish	fishery	3 600	8 600	3 200	90	410	100	0	0	99	16 000
	birds	130	180	84	150	30	0	0	0	0	570
	seals	1 600	220	18	740	800	0	0	0	0	3 300
salmon	fishery	740								40	780
	birds	1								0	1
	seals	370								110	470
sea trout	fishery	15	160	260	44	6	20	97	48	23	670
	birds	0	0	0	0	0	0	0	0	0	0
	seals	0	170	0	590	0	830	91	86	0	1 800
smelt	fishery	0	0	37	0	1 600	8	350	140	300	2 400
	birds	0	0	48	0	17	0	88	0	0	150
	seals	0	0	0	0	8	11	120	210	23	370
eel	fishery	560									560
	birds	340									340
	seals	0									0
perch	fishery	980	41	280	270	1 000	790	1 500	350	990	6 200
	birds	290	1 900	510	1 500	810	2 100	860	23	920	8 900
	seals	0	86	0	300	0	1 700	120	25	130	2 300
northern pike	fishery	54	75	9	400	140	410	450	150	1 100	2 700
	birds	0	140	0	580	19	63	84	3	24	920
	seals	0	130	0	440	0	420	0	0	0	990
pike-perch	fishery	180	22	500	130	78	240	120	9	310	1 600
	birds	0	0	190	0	180	380	0	0	110	860
	seals	0	0	0	0	0	0	0	0	0	0
whitefish	fishery	30	36	0	140	4	190	370	490	210	1 500
	birds	0	0	0	0	0	0	98	20	0	120
	seals	0	86	0	300	0	830	560	200	110	2 100
un-specified	fishery	1 400	130	860	210	610	420	410	1 500	1 700	7 200
	birds	4 000	2 200	5 300	4 600	3 600	8 900	4 900	5 300	5 400	44 000
	seals	860	820	8	2 800	580	9 200	680	10 000	520	25 000
all species	fishery										690 000
	birds										83 000
	seals										98 000

Table 2. Perch and pike catch (Table S3.4) and consumption by seals and cormorants (Tables S1.7 and S2.7) in different areas, calculated for bottoms down to 10 m based on hypsographic data (Al-Hamdani and Reker, 2007).

ICES SD	area <10 m, km^2	catch and consumption, kg/km^2							
		perch				pike			
		human	seal	cormorants	total	human	seal	cormorants	total
24	3 000	320	0	97	420	18	0	0	18
25	1 400	29	62	1 300	1 400	54	94	100	250
26	3 200	87	0	160	250	3	0	0	3
27	3 200	84	94	490	670	130	140	180	450
28	3 900	260	0	210	470	37	0	5	42
29	11 000	73	150	190	420	38	39	6	83
30	5 700	260	21	150	440	78	0	15	93
31	6 800	52	4	3	58	22	0	1	22
32	5 600	180	24	170	370	190	0	4	190
total	44 000	140	53	230	420	63	23	21	110

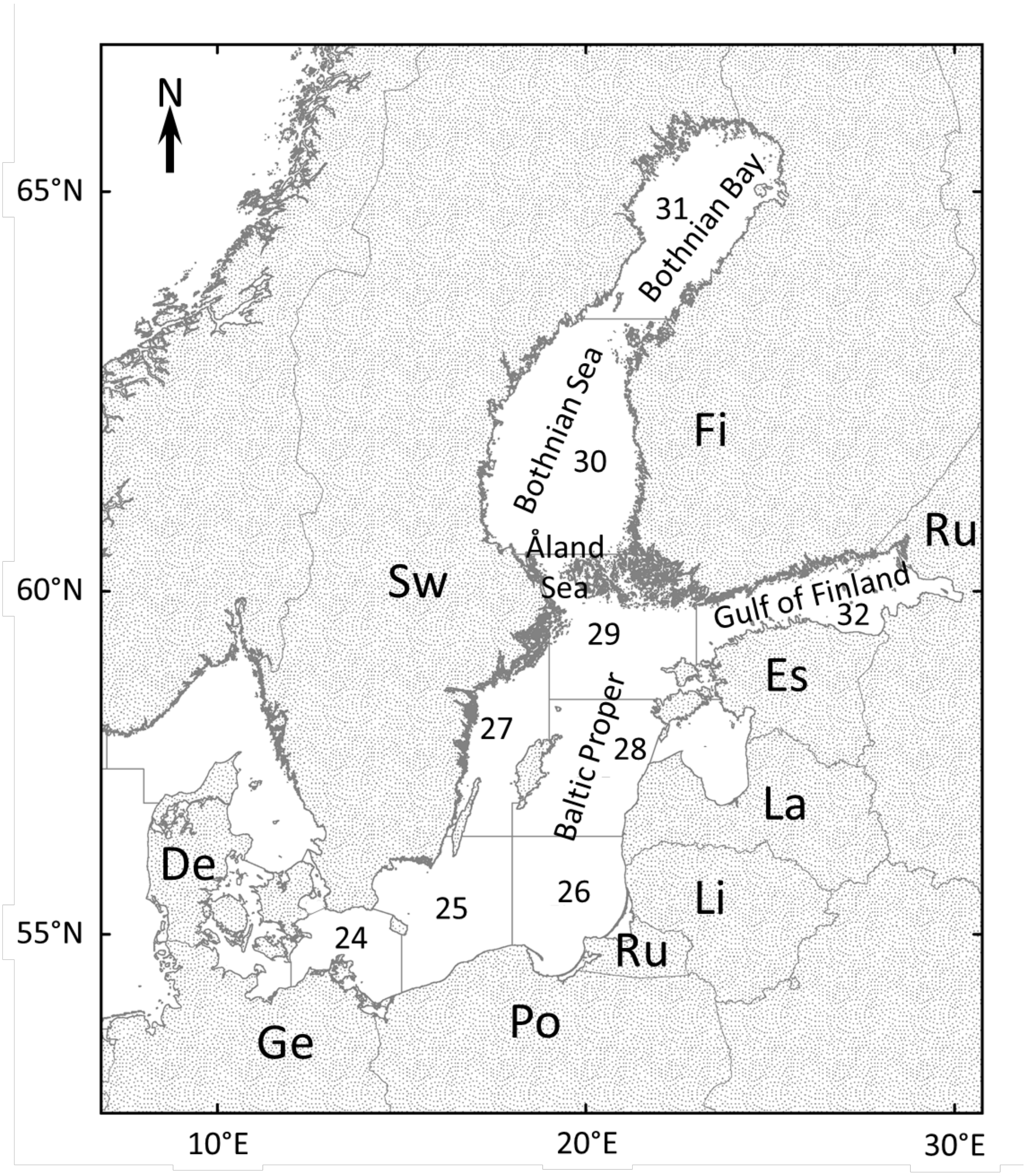

Figure 1. The Baltic Sea, with the subdivisions (SD) defined by the International Council for the Exploration of the Sea (ICES) and geographic names used in the article. Country abbreviations: De=Denmark, Es=Estonia, Fi=Finland, Ge=Germany, La=Latvia, Li=Lithuania, Po=Poland, Ru=Russia, Sw=Sweden

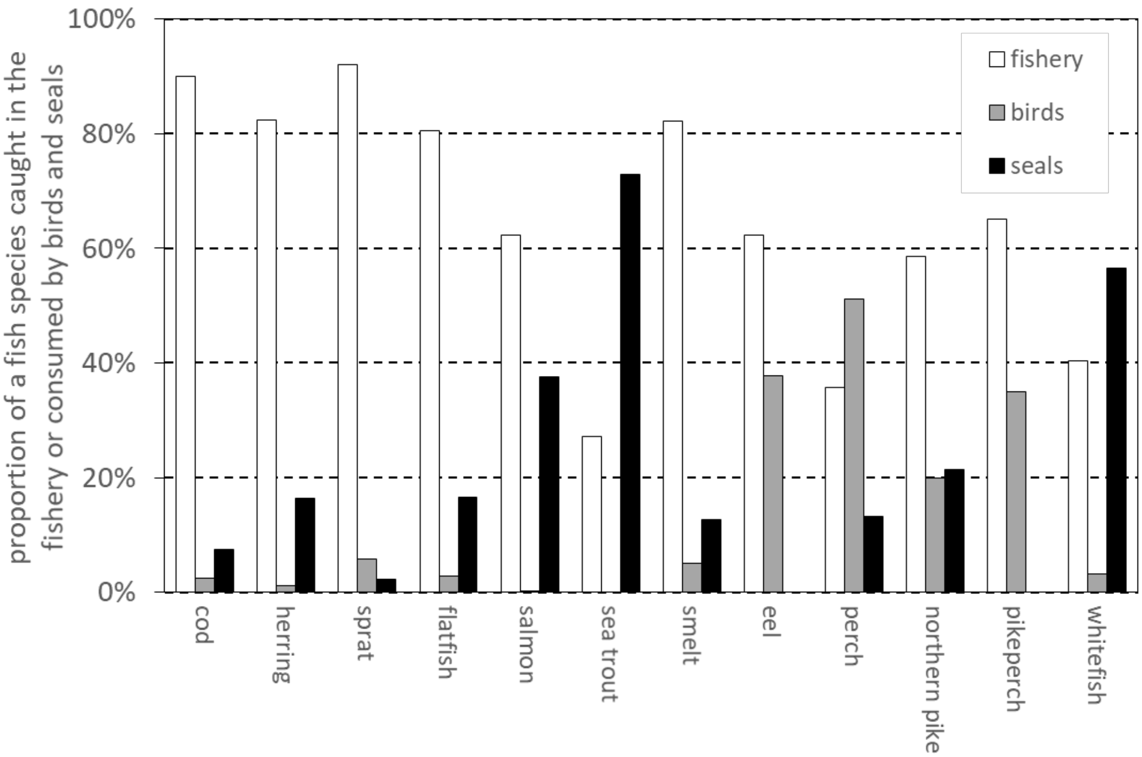

Figure 2. Proportions of different fish species extracted from the Baltic Sea through fishery catch and predation by birds and seals

Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 1 – Fish consumption by aquatic mammals

To make the calculations transparent, data are presented with an excessive number of significant figures, which are rounded off in the main text.

Abundances

Fish eating mammals in the Baltic, besides three seal species (grey seal *Halichoerus grypus*, harbour seal *Phoca vitulina* and ringed seal *Pusa hispida*), are common otter (*Lutra lutra*), American mink (*Neovison vison*) and harbor porpoise (*Phocoena phocoena*).

There are no available published data on the abundance of mink and otters. An estimate of the mink population was derived from a minimum home range area of 12 ha per mink in the Finnish archipelago (Salo et al., 2010). Converted to coastline, yields a maximum of 0.63 mink per kilometer of coast (Salo et al., 2010). Assuming the same mink density along the 38 628 km of the Swedish coastline (SCB Statics Sweden) results in an estimate of 24 300 minks. For a comparison, the highest annual hunting report of mink in Sweden was 48 200 individuals in 1988 including all freshwater habitats (Carlsson et al., 2010). The Swedish mink population is assumed to constitute one third of the total Baltic population, which is thus 73 000 animals.

The otter has increased in the Baltic Sea area during the last two decades, and expanded from freshwater habitats towards the coasts in especially the eastern parts. Today the population is estimated to roughly 2 500 individuals in the entire Finland, the main part of the population occurring in the fresh water areas (HELCOM, 2013).We assume a population of at most 1 000 individuals in the Baltic.

Harbor porpoises in the Baltic have been surveyed from air twice over the last decades. In 1995 the estimated population amounted to 200-3300 specimens (95% confidence intervals, Berggren et al., 2002) whereas a survey in 2002 estimated the population to 10-460 individuals roughly in areas SD 24 and SD 25 (Berggren et al., 2004). The lower option is unrealistic, why we use the figure 460 individuals. The project SAMBAH – Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise – has estimated the population abundance but final corrected data is not published yet. Especially in SD 24 the estimate will exceed earlier estimates considerably (SAMBHA, 2016). Several fish species is consumed by porpoises in western Baltic, but gadoids and clupeids dominate (Lockyer and Kinze, 2003; Sveegaard et al., 2012).

All three species of seals are surveyed during peak moulting season, when the largest proportion of the population is hauled out. Consequently, numbers of counted seals provide robust index data for trend analyses, but for estimates of true population size conversion factors have to be applied.

Moulting ringed seals are scattered on the ice in late April and are assessed using a strip survey technique, where north-southerly strips are flown such that a minimum of 13% of the total ice area is covered (Härkönen and Lunneryd, 1992). In the Bothnian Bay, counts increased from 4 900 in 2005 to 8 000 in 2013 (Härkönen et al., 2012; Härkönen et al., 2013). In the Finnish Archipelago Sea, the Gulf of Finland, and the Gulf of Riga, surveys have been sporadic due to variable ice conditions. In 2012, 150 ringed seals were recorded in the Archipelago Sea (Markus Ahola, Natural Resources Institute Finland, pers. comm.) and 100 specimens in the Gulf of Finland (Michail Verevkin, University of St. Petersburg, Russia, pers. comm.). In the Gulf of Riga and Estonian coastal waters ringed seal populations are stable or declining after 1996 (Mart Jussi, Estonian Fund for Nature, Estonia, pers. com.), when 1 500 were counted (Härkönen et al., 1998). Consequently, our best estimate of the hauled out population of Baltic ringed seals is 9 750. The hauled out fraction is not known, but surveys in 2015 showed that numbers of hauled out seals in the Bothnian Bay amounted to about 17 000, when winter lairs had collapsed (Härkönen unpublished data). Consequently, the haul-out fraction in earlier counts should have been below 50%. Thus the minimum true population size in this area should amount to 20 000 ringed seals in 2013, and at least 2 100 ringed seals in the Estonian coastal waters, and about 300 seals in the Archipelago Sea and 200 in the Gulf of Finland.

The peak haul-out season for grey seals occur in the last week of May and the first week of June, when coordinated international surveys are carried out in Estonia, Finland, Russia, and Sweden since year 2000. The haul-outs are generally surveyed twice during the two-week period and numbers are reported for each basin. Total numbers of counted seals have increased from about 18 000 in 2005 to 30 000 in 2013. However, the population in the Bothnian Bay is stagnant, whereas numbers increase in the Baltic Proper. As for ringed seals, there is no accurate data on the fraction hauling out during surveys, but best available information (Hiby et al., 2007) suggest that 60-80% of the population is visible during surveys, and if a 70% correction factor is applied, the total Baltic grey seal population amount to about 43 000 seals in 2013.

The peak haul-out season for harbour seals occurs in mid-August in the Kalmarsund region and during the last two weeks of August in the southern Baltic (Heide-Jørgensen and Härkönen, 1988). During these periods, each area is surveyed three times. With more information on the harbour seals than for the other species, the fraction hauled out during surveys has been estimated 56% of the average count and 65% of trimmed mean values, where mean is based on the two highest counts. In 2005 there were at most 450 seals counted in the Kalmarsund region and in 2013 the corresponding number was 950 seals (Härkönen and Isakson (2010), Härkönen unpubl.). In the southern Baltic, the maximum numbers of counted harbour seals amounted to 581 in 2005, and 940 in 2013 (Härkönen unpubl.). From these observations we estimate the total harbour seal population in the Baltic to 2 900 individuals in 2013.

Abundances of mammals are shown in Table S1.1, and for seals we also give estimated numbers in different areas (Table S1.2).

Food consumptions

The daily energetic intake of phocid seals shows a strong seasonal flux, with reduced feeding during the moulting, lactation (females) and mating (males) periods (Härkönen and Heide-Jørgensen, 1990; Lydersen and Kovacs, 1999; Mellish et al., 2000; Lidgard et al., 2005). The mean daily consumption of seals thus only gives a coarse picture, where the weight consumed also is influenced by the fat contents of the prey e.g. Winship et al. (2002). The mean daily consumption is estimated to 2.0-2.4 kg for a ringed seal (Ryg and Øritsland, 1991; Lundström et al., 2014), 3.7-4.6 kg for a harbour seal (Härkönen and Heide-Jørgensen, 1991), and 4.5-5.0 kg for a grey seal (Hammond and Grellier, 2006; Hammond and Harris, 2006). Using mean values of these estimates gives annual per capita consumptions at 800 kg for ringed seals, 1530 kg for harbour seals, and 1750 kg for grey seals.

Otter (Nolet and Kruuk, 1994; Kruuk, 2006) and harbour porpoise (Lockyer, 2003; Lockyer et al., 2003) are assumed to feed only on fish and have annual individual consumptions of 440 and 1450 kg respectively. The diet of mink is more mixed and we assumed 1/3 to be fish (Dunstone, 1993; Hammershøj et al., 2004; Salo et al., 2010), resulting in an annual individual fish consumptions of 18 kg.

Diets

Since seals consume at least 95% of the fish eaten by aquatic mammals based on the data in Table S1.1, only these three species are considered in further analyses. Seals are generally opportunistic feeders and their diets vary considerably by area, year, season and age group (Söderberg, 1975; Härkönen, 1987; Härkönen and Heide-Jørgensen, 1991; Lundström et al., 2010; Lundström et al., 2014). With reasonably many observations and good spatial and temporal coverage it is however possible to derive general patterns of diet compositions. Most of the diet samples were collected in coastal areas which may have introduced some bias in diets, overestimating the proportions of coastal fish species. Current information about seal diets in the Baltic has been determined from analyses of prey remains (mostly bones and otoliths) in digestive tracts and scats. We used results from Lundström et al. (2014) for ringed seals in the Bothnian Bay (n=43, ICES SD31), supported by Suuronen and Lehtonen (2012), whereas the diet of ringed seals in other areas was assumed to be similar, except for the replacement of vendace by sprat (Tormosov and Rezvov, 1978). For harbour and grey seals in ICES SD24 we used results from Andersen et al. (2007) (n=26), assuming that harbour and grey seals have similar diets. For grey seals in ICES SD26 and SD28 we used unpublished data from a dietary study based on scats (n=112) collected off Gotland 2011-2012 (Lundström and Asp in prep). For grey seals in ICES SD27, SD29, SD30-32, we used data from digestive tract contents from hunted seals (n=624) between 2001 and 2013 (Lundström et al. in prep.). The recovery, identification and quantification of prey remains followed the procedures described in Lundström et al. (2007); Lundström et al. (2010). Grey seals and harbour seals in ICES SD25 were assumed to have the same diet as grey seals in SD27.

Diet compositions used in our calculations are summarized in Tables S1.3-S1.5

Table S1.1. Abundances of mammals in the Baltic Sea in 2013 and annual individual and population food consumption.

Species	Total number in the Baltic Sea	Individual fish consumption per year (kg)	Total annual fish consumption (metric tons)
grey seal	43000	1750	75250
harbour seal	2900	1530	4437
ringed seal	22600	800	18080
common otter	1000	440	440
American mink	73000	18	1314
harbor porpoise*	460	1450	667
total			100188

* SD24 and SD25

Table S1.2. Seal abundances in different parts of the Baltic Sea in 2013, referring to ICES subdivisions (SD) shown in Figure 1.

Area, ICES subdivisions	Abundance, number per SD		
	grey seal	harbour seal	ringed seal
24	2400†	2900†	0
25			0
26	50	0	0
27 and 29 Swedish area	16900‡	0	0
29 Finnish area	13050	0	300
28 and islands in southeastern 29	4500ϕ	0	2100ϕ
30	3500	0	300
31	1400	0	19700
32	1200	0	200
total	43000	2900	22600

† in consumption analyses, equal distribution assumed between SD24 and 25
‡ in consumption analyses, equal distribution assumed between SD27 and 29
ϕ in consumption analyses, equal distribution assumed between SD28 and 29

Table S1.3. Grey seal diet proportional compositions by weight in different parts of the Baltic Sea. Figures in brackets indicate sample size in underlying diet studies.

Prey species	ICES subdivision (number of analysed seals)								
	SD24*	SD25	SD26	SD27 (n=59)	SD28 (n=112)	SD29 (n=92)	SD30 (n=223)	SD31 (n=218)	SD32 (n=32)
Herring *Clupea harengus*	7%	Same as in SD27	Same as in SD28	43%	29%	56%	67%	74%	45%
Sprat *Sprattus sprattus*	1%			13%	4%	10%	3%	0%	10%
Unknown Clupeidae	0%			0%	1%	3%	0%	0%	4%
Cod *Gadus morhua*	36%			10%	36%	0%	0%	0%	0%
Burbot *Lota lota*	0%			0%	0%	0%	0%	1%	0%
Salmon *Salmo salar*	0%			0%	0%	0%	3%	1%	2%
Sea trout *S. trutta*	0%			1%	0%	1%	1%	1%	0%
Salmo spp	0%			2%	0%	1%	1%	2%	0%
Unknown Salmonidae	0%			1%	0%	0%	1%	3%	3%
Common white-fish *Coregonus* sp.	0%			2%	0%	2%	9%	7%	5%
Vendace *Coregonus albula*	0%			0%	0%	0%	0%	2%	0%
Coregonus spp	0%			0%	0%	0%	0%	1%	0%
Smelt *Osmerus eperlanus*	0%			0%	0%	0%	2%	2%	1%
Perch *Perca fluviatilis*	0%			2%	0%	2%	2%	1%	6%
Unknown Percidae	0%			0%	0%	2%	0%	0%	0%
Eelpout *Zoarces viviparus*	2%			6%	0%	9%	4%	1%	7%
Gobiidae	0%			0%	0%	1%	1%	0%	0%
Ammodytidae	10%			3%	0%	0%	1%	0%	0%
Pike *Esox lucius*	0%			3%	0%	1%	0%	0%	0%
Flatfish	36%			5%	20%	0%	0%	0%	0%
Sculpins	0%			0%	2%	0%	2%	1%	0%
Cyprinidae	3%			8%	0%	6%	1%	0%	7%
Unspecified	5%			2%	7%	5%	1%	2%	8%

*Assumed to be similar to the diet of harbour seals in SD24

Table S1.4. Ringed seal diet proportional compositions in different parts of the Baltic Sea. Figures in brackets indicate sample size in underlying diet studies

Prey species	SD28-30, 32	SD31 (n=43)
Herring	37%	37%
Sprat	36%	0%
Vendace	0%	36%
Smelt	1%	1%
Eelpout	3%	3%
Fourhorned sculpin	2%	2%
Three-spined stickleback	21%	21%
Unspecified	1%	1%

Table S1.5. Harbour seal diet proportional compositions in different parts of the Baltic Sea

ICES subdivision / Prey species	SD24‡ (n=26)	SD25*
Herring	7%	43%
Sprat	1%	13%
Cod	36%	10%
Sea trout	0%	1%
Salmo spp	0%	2%
Unknown Salmonidae	0%	1%
Common whitefish	0%	2%
Perch	0%	2%
Eelpout	2%	6%
Ammodytidae	10%	3%
Pike	0%	3%
Flatfish	36%	5%
Cyprinidae	3%	8%
Unspecified	5%	2%

‡ averaged from (Andersen et al. 2007)

*Assumed to be similar to the diet of grey seals in SD27

Table S1.6. Summary of estimated consumptions (tons) by seals, derived by combining information is Tables S1.1 – S1.5

Prey species	SD24		SD25		SD26	SD27	SD28		SD29		SD30		SD31		SD32		Total			
	Grey seal	Harbor seal	Grey seal	Harbor seal	Grey seal	Grey seal	Grey seal	Ringed seal	Grey seal	Ringed seal	Grey seal	Ringed seal	Grey seal	Ringed seal	Grey seal	Ringed seal	Grey seal	Ringed seal	Harbor seal	All three spp.
Herring	147	155	893	943	26	6285	1154	307	23462	395	4134	88	1825	5768	955	59	38880	6617	1098	46595
Sprat	21	22	267	283	4	1878	158	299	4239	384	196	85			219	826	6981	826	305	8112
Unknown Clupeidae					1		39		1247						84		1371			1371
Cod	756	799	208	216	32	1464	1433										3893		1015	4908
Burbot													25				25			25
Salmon											190		25		42		256			256
Trout			21	22		148			416		61		25				670		22	692
Salmo spp			42	44		296			416		61		49				864		44	908
Unknown Salmonidae			21	22		148					61		74		63		367		22	389
Common whitefish			42	44		296			831		564		179		105		2016		44	2061
Vendace													49	5611			49	5611		5660
Coregonus spp													25				25			25
Smelt								8		11	123	2	49	158	21	2	193	181		373
Perch			42	44		296			831		123		25		134		1450		44	1495
Unknown Percidae									831								831			831
Eeloput	42	44	126	133		887		25	3803	32	246	7	25	473	147	5	5275	542	177	5995
Gobiidae									416		61						477			477
Ammodytidae	210	222	63	67		444					61						778		288	1066
Pike			63	67		444			416								922		67	989
Flatfish	756	799	105	111	18	739	799										2417		910	3327
Sculpins					2		79	17		22	123	5	25	315		3	228	362		589
Cyprinidae	63	67	166	177		1168			2494		61				153		4105		244	4349
Three-spined stickleback								175		225		50		3278		33		3761		3761
Unspecified	105	111	42	44	6	296	276	8	2161	11	61	2	54	158	176	2	3178	181	155	3514

Table S1.7. To compare seal consumption (tons) with human catch, Table S1.6 has been condensed to the same structure as Table S3.4

Grey seal

SD / fish species	24	25	26	27	28	29	30	31	32
cod	756	3137							
herring[1]	147	32910					4134	1825	1024
sprat[1]	7192								
flatfish	756	105	18	739	799				
salmon[2]	368								105
sea trout[2]		84		592		831	91	86	
smelt							123	49	21
eel									
perch[3]		42		296		1663	123	25	134
northern pike		63		444		416			
pikeperch									
whitefish[4]		42		296		831	564	198	105
unspecified	420	397	8	2795	354	8874	613	182[5]	477

Ringed seal

SD / fish species	24	25	26	27	28	29	30	31	32
cod									
herring		703					88	5768	59
sprat	826								
flatfish									
salmon									
sea trout									
smelt					8	11	2	158	2
eel									
perch									
northern pike									
pikeperch									
whitefish									
unspecified					225	289	64	9834[6]	43

Harbor seal

SD / fish species	24	25	26	27	28	29	30	31	32
cod	799	216							
herring	155	943							
sprat	305								
flatfish	799	111							
salmon									
sea trout[2]		89							
smelt									
eel									
perch		44							
northern pike		67							
pikeperch									
whitefish		44							
unspecified	444	422							

1 - for each SD separately, the mass of unknown clupeidae is split between herring and sprat proportionally to their masses
2 - for each SD separately, the masses of Salmo spp and unknown Salmonidae are split between salmon and trout proportionally to their masses
3 - perch is the totally dominating Percidae in seal stomachs and all unknown Percidae are assigned to perch
4 - for each SD separately, the mass of Coregonus spp is split between common whitefish and vendace proportionally to their masses
5 - of which 54 tons vendace
6 - of which 5611 tons vendace

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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 2 – Fish consumption by birds

To make the calculations transparent, data are presented with an excessive number of significant figures, which are rounded off in the main text.

Abundances and Food consumption

For birds, food consumption were based on assumed daily rations equivalent to 20% of the birds' bodyweight (Carss, 1997) and D. N. Carss pers.comm. in (Engström, 2001)). Some of the species redistribute themselves over the Baltic between summer and winter, while others completely or partially leave the area in the autumn and spend winter outside the Baltic Sea. During summer, reproduction results in substantial increases in population numbers. Based on data and assumptions on these factors for 21 bird species (Table S2.1) annual fish consumption were estimated.

The five top species in the table (great cormorant (*Phalacrocorax carbo sinensis*), razorbill (*Alca torda*), common guillemot (*Uria aalge*), common merganser (*Mergus merganser*) and red-breasted merganser (*M. serrator*) were estimated to consume 80% of all fish eaten by birds in the Baltic and details on assumptions for these species and their consumption are presented in detail in Tables S2.2 – S2.4.

Diets

Razorbills (Lyngs, 2001) and common guillemots (Hedgren, 1976; Lyngs and Durinck, 1998; Österblom and Olsson, 2002; Enekvist, 2003; Kadin et al., 2012) feed almost exclusively on clupeids, primarily on sprat and to a minor extent herring. Based on these studies we assume that sprat and herring constitute 90% and 5% of diets while other species contribute 5%.

There are only a few diet studies on merganser diets in the Baltic Sea. From Finnish archipelago areas, Bagge et al. (1973) and Lemmetyinen and Mankki (1975) reported that three-spined stickleback (*Gasterosteus aculeatus*) constituted the dominant fish prey in both red-breasted and common merganser. The other fish that they found were also primarily species that are not targeted in fisheries (e.g. roach, *Rutilus rutilus* and eelpout, *Zoarces viviparous*) although occasional pike and herring were also recorded. For common merganser in the Lithuanian section of the Curonian Lagoon, Zydelis and Kontautas (2008) reported that >80% of identified prey fish biomass was smelt (*Osmerus eperlanus*) with an average size of 17 cm. Birds are also known to feed substantially on smelt during their spawning in the eastern Gulf of Finland (SD32, Dmitry Sendek pers. obs.). Studies on diets of mergansers outside the Baltic Sea shows that red-breasted merganser feed primarily on smaller fish (mainly <10 cm, (Feltham, 1990; Feltham, 1995; Bur et al., 2008; Craik et al., 2011)) than common merganser (prey fish up to 25-30 cm, (Kålås et al., 1993; McCaw III et al., 1996)). With the limited diet data availability for the mergansers, we were unable to split their consumption among different prey species.

The size of cormorant prey is considerably larger than those of the other piscivorous birds, with some studies reporting prey regularly exceeding 30 cm (Pūtys, 2012; Östman et al., 2013; Salmi et al., 2015) and preference for fish larger than 25 cm have been reported (Skov et al., 2014). The diet of the cormorant varies substantially among the numerous studies that has been conducted (Figure S2.1, Table S2.5). Based on Table S2.5, we derived diets for different areas of the Baltic (Table S2.6) and from these diets and area specific consumption (Table S2.7), consumption of different fish species were calculated.

Table S2.1. Summary of fish eating birds in the Baltic Sea and their annual consumption of fish (metric tons). Birds born during the year are referred to as young-of-the-year (YOY) individuals. The table was compiled by Henri Engström and can be referred to as 'H. Engström in Hansson et al. 2017, Table S2.1 in Supplement 2'

Species	Daily food consumption (kg, 20% of body weight)	Proportion of fish in diet, in weight %	Number of non-YOY birds	Number of nesting pairs	Number of YOY birds	Species annual fish consumption (tons)
great cormorant *Phalacrocorax carbo sinensis*	0.5	1	272229	90743	181486	39971
razorbill *Alca torda*	0.14	1	244055	34865	34865	13516
common merganser *Mergus merganser*	0.28	1	68933	22978	114889	11393
common guillemot *Uria aalge*	0.2	1	134141	19163	19163	10612
red-breasted merganser *Mergus serrator*	0.22	1	74981	24994	124968	7470
black guillemot *Cepphus grylle*	0.08	0.75	155616	25936	25936	5980
herring gull *Larus argentatus*	0.22	0.2	327404	81851	245553	5512
great crested grebe *Podiceps cristatus*	0.18	0.9	48792	16264	48792	2134
common gull *Larus canus*	0.08	0.25	319154	79789	239366	1532
white-tailed sea eagle *Haliaeetus albicilla*	1.1	0.5	5983	855	1710	1431
great black-backed gull *Larus marinus*	0.36	0.2	40460	10115	15173	941
arctic tern *Sterna paradisaea*	0.02	0.9	181654	90827	272481	834
grey heron *Ardea cinerea*	0.28	0.75	15536	3884	11652	783
lesser black-backed gull *Larus fuscus*	0.16	0.4	44933	14978	44933	604
common tern *Sterna hirundo*	0.02	0.9	44290	22145	66435	203
caspian tern *Sterna caspia*	0.2	1	3350	1675	3350	141
osprey *Pandion haliaetus*	0.4	1	978	489	1467	100
sandwich tern *Sterna sandvicensis*	0.06	0.9	2908	1454	4362	40
parasitic jaeger *Stercorarius parasiticus*	0.1	0.75	2060	1030	3090	39
red-throated loon *Gavia stellata*	0.3	1	555	185	370	38
little tern *Sterna albifrons*	0.02	0.75	4256	2128	6384	16
estimated total consumption by birds						103290

Data sources:
Abundances: Ottosson et al. (2012.), Tucker et al. (1994), Bregnballe et al. (2014), Skov et al. (2011) pers. comm. with Martin Green, Swedish Bird Survey, Lund University, Sweden; Kjell Larsson, Linneaus University, Kalmar, Sweden; Christof Herrmann, Agency for Environment, Germany; Thomas Bregnballe, Aarhus University, Denmark; Kalev Rattiste, Estonian University of Life Sciences, Estonia; http://www.luomus.fi/en/bird-monitoring, Finland.
Proportions of fish in diets: Snow and Perrins (1997), H. Engström unpubl.

Migration: Fransson and Pettersson (2001); Fransson et al. (2008) Skov et al. (2011)

Table S2.2. Duration of the summer period and proportions of the populations in the different ICES subdivisions during summer/winter periods. Based on references cited in Table S2.1. The table was compiled by Henri Engström and can be referred to as ‘H. Engström in Hansson et al. 2017, Table S2.2 in Supplement 2’

Species	Summer period	Proportion per SD, summer/winter								
		SD24	SD25	SD26	SD27	SD28	SD29	SD30	SD31	SD32
great cormorant	Mar. 16 - Sep. 15	0.11 / 0.52	0.11 / 0.06	0.13 / 0.22	0.16 / 0.07	0.10 / 0.02	0.16 / 0.11	0.11 / 0.00	0.003 / 0.00	0.12 / 0.00
razorbill	Mar. 1 - Jul. 31	0.03 / 0.15	0.00 / 0.30	0.00 / 0.20	0.27 / 0.15	0.00 / 0.20	0.36 / 0.00	0.11 / 0.00	0.17 / 0.00	0.06 / 0.00
common merganser	Apr. 1 - Oct. 31	0.00 / 0.20	0.00 / 0.05	0.00 / 0.24	0.05 / 0.17	0.02 / 0.15	0.41 / 0.16	0.14 / 0.00	0.27 / 0.00	0.11 / 0.03
common guillemot	Mar. 1 - Jul. 31	0.14 / 0.15	0.00 / 0.30	0.00 / 0.20	0.69 / 0.15	0.00 / 0.20	0.10 / 0.00	0.01 / 0.00	0.06 / 0.00	0.00 / 0.00
red-breasted merganser	Apr. 1 - Oct. 31	0.00 / 0.23	0.01 / 0.09	0.01 / 0.01	0.02 / 0.09	0.01 / 0.52	0.21 / 0.05	0.20 / 0.00	0.39 / 0.00	0.15 / 0.01

Table S2.3. Number of birds in the Baltic Sea during different periods. The period ‘Jan. 1st‘ spans Jan. 1st up to and including Jan. 15th. The birds are distributed differently during summer and winter (see Table S2.2) and winter periods are indicated with a gray background. Birds born during the year are in the ‘YOY’ (young-of-the-year) columns, where also assumed date of birth are indicated. The table was compiled by Henri Engström and can be referred to as ‘H. Engström in Hansson et al. 2017, Table S2.3 in Supplement 2’

Species	great cormorant		razorbill		common merganser		common guillemot		red-breasted merganser	
Age group / Date	older	YOY	older	YOY	older	YOY	older	YOY	older	YOY
Jan. 1st	26554		244055		55350		134141		16815	
Jan. 16th	26554		244055		55350		134141		16815	
Feb. 1st	26554		244055		55350		134141		16815	
Feb. 15th	26554		244055		55350		134141		16815	
Mar. 1st	26554		244055		55350		134141		16815	
Mar. 16th	272229		244055		55350		134141		16815	
Apr. 1st	272229		244055		68933		134141		74981	
Apr. 16th	272229		244055		68933		134141		74981	
May 1st	272229	181486	244055		68933		134141		74981	
May 16th	272229	181486	244055		68933		134141		74981	
Jun. 1st	272229	181486	244055	34865	68933	114889	134141	19163	74981	
Jun. 16th	272229	181486	244055	34865	68933	114889	134141	19163	74981	
Jul. 1st	272229	181486	244055	34865	68933	114889	134141	19163	74981	124968
Jul. 16th	272229	181486	244055	34865	68933	114889	134141	19163	74981	124968
Aug. 1st	272229	181486	278920		68933	114889	153304		74981	124968
Aug. 16th	272229	181486	278920		68933	114889	153304		74981	124968
Sep. 1st	272229	181486	278920		68933	114889	153304		74981	124968
Sep. 16th	26554		278920		68933	114889	153304		74981	124968
Oct. 1st	26554		278920		68933	114889	153304		74981	124968
Oct. 16th	26554		278920		68933	114889	153304		74981	124968
Nov. 1st	26554		278920		55350		153304		16815	
Nov. 16th	26554		278920		55350		153304		16815	
Dec. 1st	26554		278920		55350		153304		16815	
Dec. 16th	26554		278920		55350		153304		16815	

Table S2.4. Annual consumption (ton) by the five major fish eating birds in different subdivisions (SD, Figure 1) of the Baltic Sea. Calculations based on individual daily consumption (Table S2.1), their distributions over the sea (Table S2.2) and the number of birds during different periods of the year (Table S2.3). The table was compiled by Henri Engström and can be referred to as 'H. Engström in Hansson et al. 2017, Table S2.4 in Supplement 2'

	Annual fish consumption per SD								
Species	SD 24	SD 25	SD 26	SD 27	SD 28	SD 29	SD 30	SD 31	SD 32
great cormorant	5382	4277	5412	6123	3805	6219	4132	113	4508
razorbill	1364	2397	1598	2690	1598	1989	608	939	332
common merganser	468	117	562	850	532	4086	1267	2444	1066
common guillemot	1548	1882	1255	3935	1255	434	43	260	0
red-breasted merganser	128	119	75	189	360	1479	1382	2696	1042

Table S2.5. Summary of feeding data for cormorant, expressed as weight percentages in the diet. Based on analyses of stomachs from dead birds (s), more or less intact regurgitated fish (f) and regurgitated pellets with fish remains (p).

Area	A	B	C	C	O	O	P	Q	D	E	F	K	G	I	J	H	L, M	M	N
ICES SD	24	25	25	25	26	26	26	26	27	27	27	29	30	30	30	31	32	32	32
number of observations (s=stomachs, p=pellets, f=reguirigitated fish)	96p	624s	120p	430p	220p	1032p	?p	2089p 4201f	279p	195s	75kg of fish	1196p 103s 3509f	333p	30p	469p 8s 2177f	60p	286p	3046f	124p 128s
cod *Gadus morhua*	20%	13%		4%						5%	9%								
herring *Clupea harengus*	7%	2%				1%		4%		9%	7%	8%	33%	4%	19%	3%	5%	2%	5%
sprat *Sprattus sprattus*		<.5%								<.5%			<.5%						
flounder + plaice, *Platichthys flesus, Pleuronectes platessa;*	2%	12%				3%	3%			7%								<.5%	<.5%
salmon *Salmo salar*																1%			
sea trout *S. trutta*																			
smelt *Osmerus eperlanus*						3%		1%					4%		2%				1%
eel *Anguilla anguilla*	5%	3%	2%	<.5%				1%		1%	<.5%								<.5%
perch *Perca fluviatilis*	5%	15%	55%	59%	17%	16%		5%	45%		30%	33%	21%	24%	17%	20%	41%	17%	3%
pike *Esox lucius*		9%		1%					3%		25%	1%	1%	4%	1%	3%			2%
pikeperch *Sander lucioperca*					6%	5%		4%			1%	6%	<.5%		1%			4%	3%
whitefish *Coregonus* sp. excl. *C. albula*		<.5%									1%		1%	4%	2%	18%	1%		
eelpout *Zoarces viviparus*	19%	9%	3%	3%		2%	12%	5%	4%	28%	14%	9%	19%		15%		5%	24%	32%
roach *Rutilus rutilus*	9%	9%	35%	12%	42%	37%		9%	34%	2%	3%	15%		4%	18%		17%	43%	31%
other cyprinids		5%	3%	4%	6%	10%		3%	3%	10%	1%	12%	5%	8%	3%	3%	12%	4%	3%
ruffe *Gymnocephalus cernua*		2%	1%		14%	17%		69%	3%	<.5%	5%	6%	7%	30%	19%	35%	8%	2%	1%
sticklebacks *Gasterosteus aculeatus*	3%	8%					11%			30%	<.5%	1%		3%	1%	2%	1%	<.5%	2%
unspecified	29%	13%	2%	16%	15%	6%	75%	<.5%	8%	8%	3%	8%	9%	19%	2%	15%	9%	4%	16%
References	1	2,3	4	5	6	7	8	9	4	2,10	3	11-13	14	13,15	12,13	13,15	13,15	16	17

References: 1= Hald-Mortensen (1995); 2= Östman et al. (2013); 3= Ovegård, M. unpublished,; samples kindly provided by Claes Kyrk; 4= Lindell (1997), proportions calculated from numbers of fish and their average size, as given by Lindell; 5= Jonsson (1979); 6= Švažas et al. (2011); 7= Pūtys (2012);8= Bzoma and Meissner (2005); 9= Stempniewicz et al. (2003); 10= Boström et al. (2012); 11= Salmi et al. (2015); 12= Salmi et al. (2013); 13= Salmi, J.A. unpublished; 14= Bostrom et al. (2012); 15= Salmi (2011), recalculated with length-weight equation from Salmi et al. (2015); 16= Lehikoinen et al. (2011); 17= Eschbaum et al. (2003)

Table S2.6. Cormorant proportional diets in different ICES subdivisions, calculated as mean values from Table S2.5

ICES SD Prey	24	25	26	27	29	30	31	32
cod	20%	6%		5%				
herring	7%	1%	1%	5%	8%	19%	3%	4%
sprat		<.5%		<.5%		<.5%		
flounder + plaice	2%	4%	2%	2%				
salmon							1%	
sea trout								
smelt			1%			2%		
eel	5%	2%	<.5%	<.5%				
perch	5%	43%	9%	25%	33%	21%	20%	20%
pike		3%		9%	1%	2%	3%	1%
pikeperch			4%	<.5%	6%	<.5%		2%
whitefish		<.5%		<.5%		2%	18%	
eelpout	19%	5%	5%	15%	9%	11%		20%
roach	9%	19%	22%	13%	15%	7%		30%
other cyprinids		4%	5%	5%	12%	5%	3%	6%
ruffe		1%	25%	3%	6%	19%	35%	4%
sticklebacks	3%	3%	3%	10%	1%	1%	2%	1%
unspecified	29%	10%	24%	6%	8%	10%	15%	9%

Table S2.7. Annual consumption (tons) in different areas of the Baltic, expressed as ICES subdivisions). To compare bird's consumption with human catch, the table has been condensed to the same structure as Table S3.4

Cormorant

fish species \ SD	24	25	26	27	28[1]	29	30	31	32
cod	1060	532							
herring[2]	359	1096					767	3	187
flatfish	130	175	84	147	30				
salmon	1								
smelt			48		17		88		
eel	337								
perch	294	1850	514	1548	813	2073	857	23	923
northern pike		143		582	19	63	84	3	24
pikeperch			193		183	377			105
whitefish							98	20	
unspecified	3278	1764	4512	3223	2568	3204	2238	62	3269

Razorbill

fish species \ SD	24	25	26	27	28	29	30	31	32
herring	68	514					30	47	17
sprat	12164								
unspecified	68	120	80	135	80	99	30	47	17

Common guillemot

fish species \ SD	24	25	26	27	28	29	30	31	32
herring	77	438					2	13	0
sprat	9551								
unspecified	77	94	63	197	63	22	2	13	0

Common merganser

fish species \ SD	24	25	26	27	28	29	30	31	32
unspecified	468	117	562	850	532	4086	1267	2444	1066

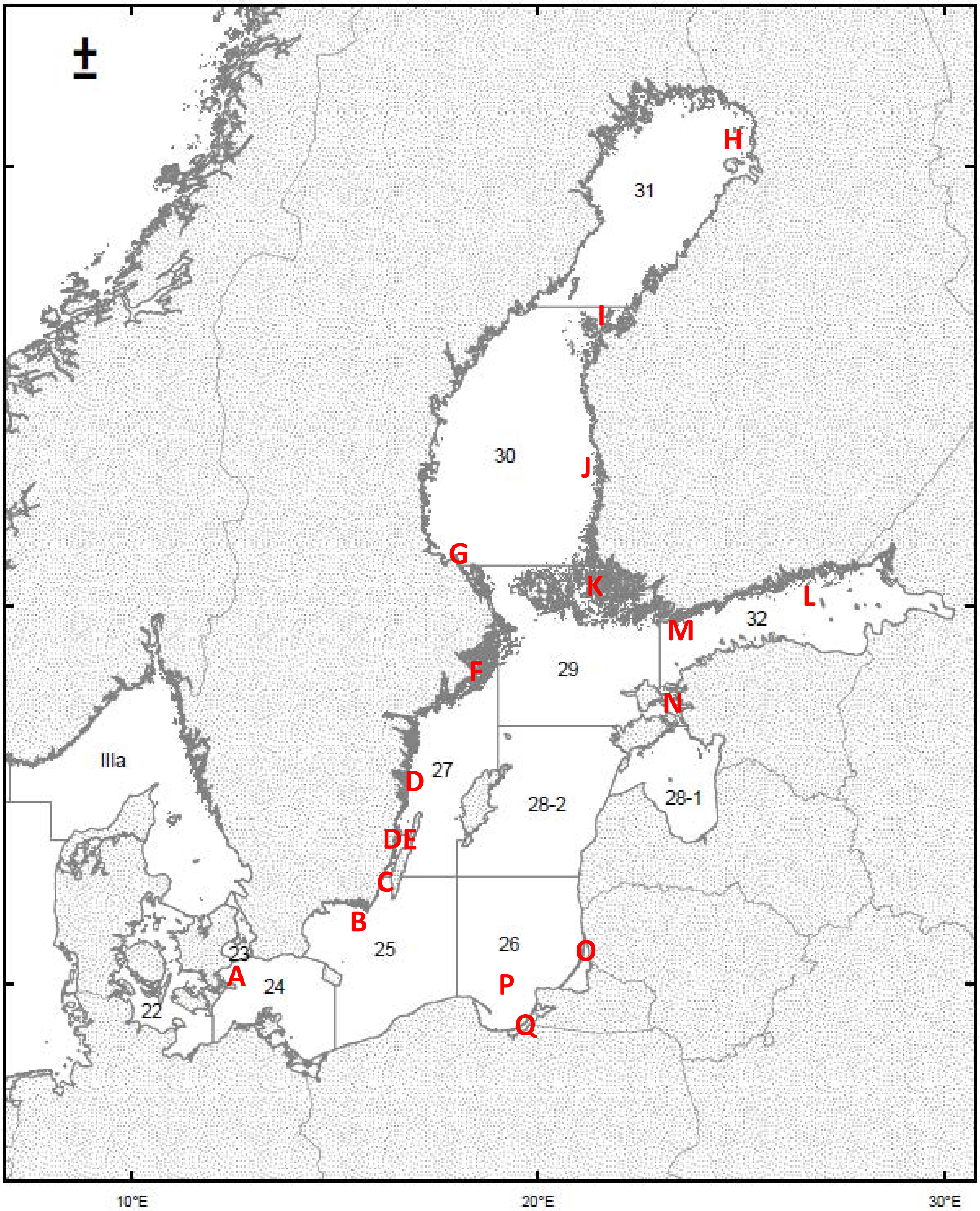
Red-breasted merganser

fish species \ SD	24	25	26	27	28	29	30	31	32
unspecified	128	119	75	189	360	1479	1382	2696	1042

1 - diet in SD28 assumed to be the average of those in SD26 and SD29

2 - all clupeids in SD32 assumed to be herring, since sprat generally contributes only marginally to the diet

Figure S2.1. Sites from where cormorant diet data have been compiled in Table S2.5



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Competition for the fish - fish extraction from the Baltic Sea by humans, aquatic mammals and birds

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Supplement 3 – Fishery catch

To make the calculations transparent, data are presented with an excessive number of significant figures, which are rounded off in the main text.

Data on commercial catch per subdivision for year 2010 were extracted from the official national catch statistics collated by ICES (www.ices.dk) and are summarized in Table S3.1. For recreational fishing there are no complete catch statistics, but various assessments are available, primarily from areas with archipelagos where there are local populations of reasonably sedentary species. From Finland and Sweden data based on postal questionnaires are available from 2010. For Finland the methods and results are described in Anon. (2011). Data for Sweden were obtained from the Swedish Agency for Marine and Water Management and the methodology is described in Thörnqvist (2009). However, these recreational catch were merged for SD24-SD25 and SD27-SD29 respectively. To allocate catch to different subdivisions they were split proportionally to Swedish commercial catch in corresponding areas. Russian data from the Gulf of Finland are averages from 2003-2008 (Anon., 2009) and are relevant also for the current situation (D. Sendek, unpubl.). For Estonia data were available from 2012, for gillnet catch from mandatory catch reports and for other types of gears estimates from a telephone-based survey (Ender et al., 2013).

To compare catch with consumption by other marine mammals and birds, all human catch are merged in Table S3.3 and S3.4. It should be recalled, however, that these data underestimates catch in the southeastern parts of the Baltic, from where we lack data on recreational fisheries for several countries. The number of significant digits is excessive given the data uncertainty but it is kept to allow readers to follow how we have merged data.

Table S3.1. Annual commercial catch (metric tons) in the Baltic Sea 2010

SD / fish species	24	25	26	27	28	29	30	31	32
cod *Gadus morhua*	8850	31115	18822	45	96	49	1	0	2
herring *Clupea harengus*	15062	24090	22737	14539	52303	24729	71694	2090	12451
sprat *Sprattus sprattus*	2116	35476	98543	35052	92309	45256	3345	2	35375
flounder *Platichthys flesus*	3159	8168	3216	37	385	91	1	0	99
plaice *Pleuro-nectes platessa*	441	402	3	0	0	0			
salmon *Salmo salar*	55	236	59	2	4	11	83	219	38
sea trout *S. trutta*	15	110	257	2	6	10	40	22	21
smelt *Osmerus eperlanus*	0		37	0	1564	8	345	142	245
eel *Anguilla anguilla*	253	129	35	124	2	9	2	0	1
perch *Perca fluviatilis*	982	24	282	12	869	226	473	67	256
northern pike *Esox lucius*	54	8	9	8	7	57	105	30	58
pikeperch *Sander lucioperca*	180	22	498	5	78	121	100	5	156
whitefish *Coregonus* sp.	30	6	0	17	4	98	287	330	60
unspecified (of which cyprinids)	1408 (91%)	106 (33%)	855 (93%)	5 (0%)	170 (68%)	174 (96%)	273 (89%)	1258‡ (7%)	1082 (63%)

‡ = 1163 tons of vendace (*Coregonus albula*)

Table S3.2. Annual catch (tons) in recreational and household fisheries 2010 in Sweden and Finland, average 2003-2008 in Russia and 2012 in Estonia.

fish species \ SD	24	25	26	27	28	29	30	31	32
cod	11	87	no data	31	2	37	0	0	2
herring	3	8		138	122	193	178	55	175
sprat	0	0		0	0	0	0	0	10
Flounder + plaice	8	23		53	22	9	0	0	0
salmon	2	21		18	0	9	8	10	2
sea trout	0	46		42	0	10	57	26	2
eel	0	0		0	0	0	0	0	0
perch	0	17		254	130	563	1040	282	734
pike	0	67		396	138	354	342	118	996
pikeperch	0	0		127	0	123	17	4	157
whitefish	0	30		121	0	94	88	159	151
unspecified (of which cyprinids)	7 (0%)	27 (0%)		207 (0%)	443 (10%)	247 (83%)	136 (95%)	216 (50%)	656† (66%)

†=of which 56 tons of smelt

Table S3.3. Combined catch (tons) in commercial, recreational and household fisheries derived by combining Tables S3.1 and S3.2. When catch in the recreational/household fisheries were merged for two or more subdivisions, or when species were merged, these catch data were split in proportions proportional to catch in the commercial fishery.

fish species \ SD	24	25	26	27	28	29	30	31	32	24-32
cod	8861	31202	18822	76	98	86	1	0	4	59150
herring	15065	24098	22737	14677	52425	24922	71872	2145	12626	240567
sprat	2116	35476	98543	35052	92309	45256	3345	2	35385	347484
flounder	3166	8190	3216	90	407	100	0	0	99	15268
plaice	442	403	3	0	0	0	0	0	0	848
salmon	57	257	59	20	4	20	91	229	40	776
sea trout	15	156	257	44	6	20	97	48	23	666
smelt	0	0	37	0	1564	8	345	142	301	2397
eel	253	129	35	124	2	9	2	0	1	555
perch	982	41	282	266	999	789	1513	349	990	6210
northern pike	54	75	9	404	145	411	447	148	1054	2747
pikeperch	180	22	498	132	78	244	117	9	313	1593
whitefish	30	36	0	138	4	192	375	489	211	1475
unspecified	1415	133	855	212	613	421	409	1474	1682	7214
total	32636	100217	145353	51236	148654	72478	78615	5034	52729	686951

Table S3.4. For some fish, primarily open sea species, it is realistic to assume that there is a common population for the entire Baltic Sea, while other species are divided into more or less sedentary subpopulations. This difference among species are of relevance when evaluating competition between man and beasts, since local fish populations may be impacted by local predation, while the impact on basin wide populations must be analyzed based on the total predation on the species. Based on this approach, Table S3.3 has been modified to better represent catch of different populations. The merging of catch is based on the population structures applied by ICES, except that flatfish and sea trout are kept as single SD values since these species may reproduce locally and are relatively sedentary. Values represent estimated annual consumption in tons.

SD / fish species	24	25	26	27	28	29	30	31	32
cod	8861	50289							
herring	15065	151484					71872	2145	‡
sprat	347484								
flatfish	3608	8593	3219	90	407	100	0	0	99
salmon	736								40
sea trout	15	156	257	44	6	20	97	48	23
smelt	0	0	37	0	1564	8	345	142	301
eel	555								
perch	982	41	282	266	999	789	1513	349	990
northern pike	54	75	9	404	145	411	447	148	1054
pikeperch	180	22	498	132	78	244	117	9	313
whitefish	30	36	0	138	4	192	375	489	211
unspecified	1415	133	855	212	613	421	409	1474†	1682

‡ = catches in SD32 merged with those in SD25-29

†= of which 1163 ton of vendace

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Supplement 4 – Review of published studies on cormorant predation on perch

Perch is a common coastal species about which much has been published, including articles addressing possible effects of predation by cormorants.

Perch forms local populations along the coast, with genetic, growth and condition differences over short distances (Hansson, 1985; Bergek and Björklund, 2009; Bergek *et al.*, 2010; Ahlbeck Bergendahl *et al.*, 2017). These local populations are potentially responsive to changes in local exploitation pressure. Bergström *et al.* (2007) showed that perch in a 4 km^2 area closed to fisheries where both larger and more abundant than in neighbouring fished areas. This implies that coastal fisheries can be intensive enough to impact local populations to such an extent that compensatory mechanisms are insufficient to buffer this impact. With cormorants and seals in some subdivisions consuming twice as much perch as caught in fisheries (Table 1), competition is likely to occur at least locally.

Adill and Andersson (2006) quantified fish >10 cm in a typical perch habitat (depth <10m) and concluded that perch constituted 43-55% of the biomass. The perch proportion of the total fish biomass is smaller, given the high abundance of fish <10 cm (Aneer and Nellbring, 1977;

Hansson, 1984; Nellbring, 1985; Thorman, 1986). Assuming that perch still constitute a large proportion (20%) of the total fish production on bottoms <10 m, this would equal 2 tons/km^2 (assumed fish production 10 tons per km^2, see Material and Methods).

Based on our consumption estimates (Table 1) the average extraction of perch exceeds 400 kg/km^2 in potential perch habitat (Table 2). However, as a large proportion of these bottoms are located in the outer coastal zone and off-shore areas where perch is uncommon, the exploitation intensity in the archipelagos is generally substantially higher.

With an estimated perch production of 2 tons/km^2, the local fishing/predation pressure can reach or exceed the level 20-40% of the production (Table 2), which for other Baltic fish stocks have resulted in adverse impacts on the populations (see Material and Methods). Thus perch populations in the Baltic are likely to be locally negatively impacted by both fisheries, predation from cormorants and in some areas possibly also by seals.

Several field studies have addressed the possible effects of cormorant predation on the abundance of perch. Some of these publications are based on long-term data, but these sampling programs were not designed to study interactions between cormorants and fish, compromising the statistical power of analyses. Based on 15 years of fish monitoring data from the Baltic Proper, Östman *et al.* (2012) reported ~80% lower catch of perch in an area with cormorant colonies compared to a reference area that had no colonies within 50 km. In time series analyses they also found a negative association between perch abundance and the size of the cormorant colonies. Their findings are supported by modelling results presented by Östman *et al.* (2013). During the period 1998-2011, commercial perch catch in the Finnish Archipelago Sea area decreased by about 50% and Salmi *et al.* (2015) proposed that this was caused by predation by cormorants, as they increased from zero to 4000-5000 nesting pairs during the same period (see also Heikinheimo and Lehtonen, 2016; Salmi *et al.*, 2016). Using data from all Finnish coastal areas during 2002-2014, when cormorants were well established and abundant, Lehikoinen *et al.* (2017) reported generally increased perch catch. They analysed changes in catch rates in commercial fisheries vs. dynamics in cormorant numbers and found no significant relationship. Results from a short (6 years, 2005-2010) monitoring fishery in the entrance to the Gulf of Finland showed increased perch catch while the number of nesting cormorants in the area showed modest fluctuation (700-1400 nesting pairs, Lehikoinen *et al.*, 2011). A strong negative impact on perch by cormorants was suggested by Vetemaa *et al.* (2010), reporting a 90% abundance decrease in perch after the establishment of a cormorant colony in a small (~9 km^2) Estonian bay.

In a study designed specifically to explore possible effects of cormorant predation on the fish community, Gagnon *et al.* (2015) compared catch at pairs of islands with and without cormorant colonies and reported three times larger catch at islands without colonies. At islands that had been colonised for seven years or more, catch were reduced by 90%. Pūtys (2012) analysed perch catch at two monitoring stations, located 7 and 25 km from a cormorant colony in the Curonian Lagoon. During the study period the colony increased from 200 to 3800 nesting pairs, but there was no temporal trend in catch. Further, there was no correlation between catch of perch and distances (<1 to ~23 km) from the cormorant colony. The Curonian Lagoon has a maximum depth of 5 m (Paldavičienė *et al.*, 2009), which makes the entire area (1600 km^2) perch production habitat and applying the same production assumptions as above this results in a total perch production of 3200 tons, compared to 118 tons consumed by cormorants and 48 tons caught in fisheries (Pūtys, 2012). The total extraction of perch was thus only 5-6% of the estimated production. This proportion may even be overestimated, as the primary productivity in the lagoon is 2-4 times higher than in the Baltic Proper (Elmgren 1984; Aleksandrov, 2010), probably also resulting in a higher fish production. The high productivity in the Curonian Lagoon may explain the absence of a detectable impact of cormorant predation.

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